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TAXONOMIC STATUS OF *NYCTIMENE* (CHIROPTERA: PTEROPODIDAE) FROM THE BANDA, KAI AND ARU ISLANDS, MALUKU, INDONESIA - IMPLICATIONS FOR BIOGEOGRAPHY

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ABSTRACT

Nyctimene is recorded for the first time from the Aru and Banda island groups. The *Nyctimene* from Wokam, Aru island group, is morphologically close to *N. albiventer papuanus*. That from Kai Besar, Kai Kecil and Banda islands is described as a new subspecies of *N. albiventer*. The biogeographic relevance of this taxonomic separation is briefly discussed in the context of the mammal biogeography of these islands.

INTRODUCTION

Anderson (1912) first critically reviewed the genus *Nyctimene* Borkhausen and recognised 13 species. Since that time a further nine taxa have been described. These forms are distributed from the Philippines, Sulawesi, Maluku islands, Timor, north-east Australia, New Guinea and associated eastern islands.

As a consequence of the reviews and statements of Laurie and Hill (1954) Greig-Smith (1975), Koopman (1979,1982), Smith and Hood (1983), Petersen (1991), Corbet and Hill (1991, 1992) and Koopman *in* Wilson and Reeder (1993) the classification of these forms is generally considered to be as follows:

- *Nyctimene minutus* Andersen, 1910

  N. m. minutus Andersen, 1910 - Sulawesi, Obi I.

  N. m. varius Andersen, 1910 - W. Buru
- *Nyctimene albiventer* (Gray, 1863)

  N. a. albiventer (Gray, 1863) - Morotai I., Halmahera I., Ternate I.

  N. a. papuanus K. Andersen, 1910 - E. New Guinea, New Britain, Admiralty islands and Solomon islands.
- *Nyctimene draconilla* Thomas, 1922 - S. New Guinea
- *Nyctimene cephalotes* (Pallas, 1767)

  N.c. cephalotes (Pallas, 1767) - Moluccas (fixed on Ambon I. by Andersen (1912), Sulawesi, Timor I., Timor Laut I., Tanimbar islands, Buru I., Seram I., N.W. Irian Jaya - Noomfor I. and southwest Papua)

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[*Vespertilio c. melinus* (Kerr, 1872)]

[*Cephalotes pallasi* (E. Geoffrey, 1810)]

- *Nyctimene major* (Dobson, 1877)

N. m. major (Dobson 1877) - Duke of York I., Bismark Archipelago

N. m. lullulae Thomas, 1904 - Woodlark I., Tobriand islands.

N. m. geminus Andersen, 1910 - Tobriand and D'Entrecasteaux Archipelagos, Fergusson I., Kiriwia islands, Heath I., Goodenough I., Louisiade Archipelago.

N. m. scitulus Andersen, 1910 - Solomon islands: Shortland, Alu, Florida, New Guinea, Guadalcanar; Choiseul and Malapa

- *Nyctimene cyclotis* Andersen, 1910 - Arfak Mountains, Irian Jaya

N. c. certans Andersen, 1912 - S. New Guinea

- *Nyctimene aello* (Thomas, 1900) - E. New Guinea
- *Nyctimene celaeno* Thomas, 1922 - N.W. New Guinea
- *Nyctimene malaitensis* Phillips, 1968 - Malaita I., E. Solomon islands.
- *Nyctimene masalai* Smith and Hood, 1983 - New Ireland I..
- *Nyctimene rabori* Heaney and Petersen, 1984 - Negros I., Philippines
- *Nyctimene sanctacrucis* Troughton, 1931 - Santa Cruz I.
- *Nyctimene vizcaccia* Thomas, 1914

N. v. vizcaccia Thomas, 1914 - Ruk I., Bismark Archipelago; Solomon islands.

N. v. bougainville Troughton, 1936 - Bougainville I., Solomon islands.

[*N. albiventer minor* Phillips, 1968] - Fauro, Choiseul and Santa Ysabel islands.

Recent expeditions to the Banda, Kai and Aru islands collected series of small *Nyctimene* with forearm measurements about 60 mm or less. The *Nyctimene* from Kai islands were considered by Andersen (1912) to be *N. albiventer papuanus*; he included several specimens from Kai islands in the measurements he presented for this form, including one specimen from Elat, Kai Besar I. Those collected from Banda Neira I., Banda islands and Wokam I., Aru islands are the first recorded from these island groups.

This paper presents the results of an examination of the taxonomic status of the forms of *Nyctimene* from Banda, Kai, and Aru by comparison with other small forms of *Nyctimene* with which they might be confused. These are the forms: *N. minutus, N. albiventer, N. cyclotis, N. cephalotes, N. masalai* and *N. vizcaccia.*

MATERIALS AND METHODS

A total of 62 adult specimens (listed in specimens examined section)was examined. These were from Banda Neira I. (2) Dullah I./Kai Kecil (7), Kai Besar I. (5) Wokam I./Aru islands (27), the Halmahera group (6) and Papua New Guinea (15). The locality of these specimens is listed in Figure 1. Apart from the Halmahera group specimens (Australian Museum, Sydney), all specimens are currently lodged in the Western Australian Museum. At the completion of this series of surveys half of the specimens from Banda I., Kai islands and Aru islands will be lodged in the Museum Zoologicum Bogoriense.

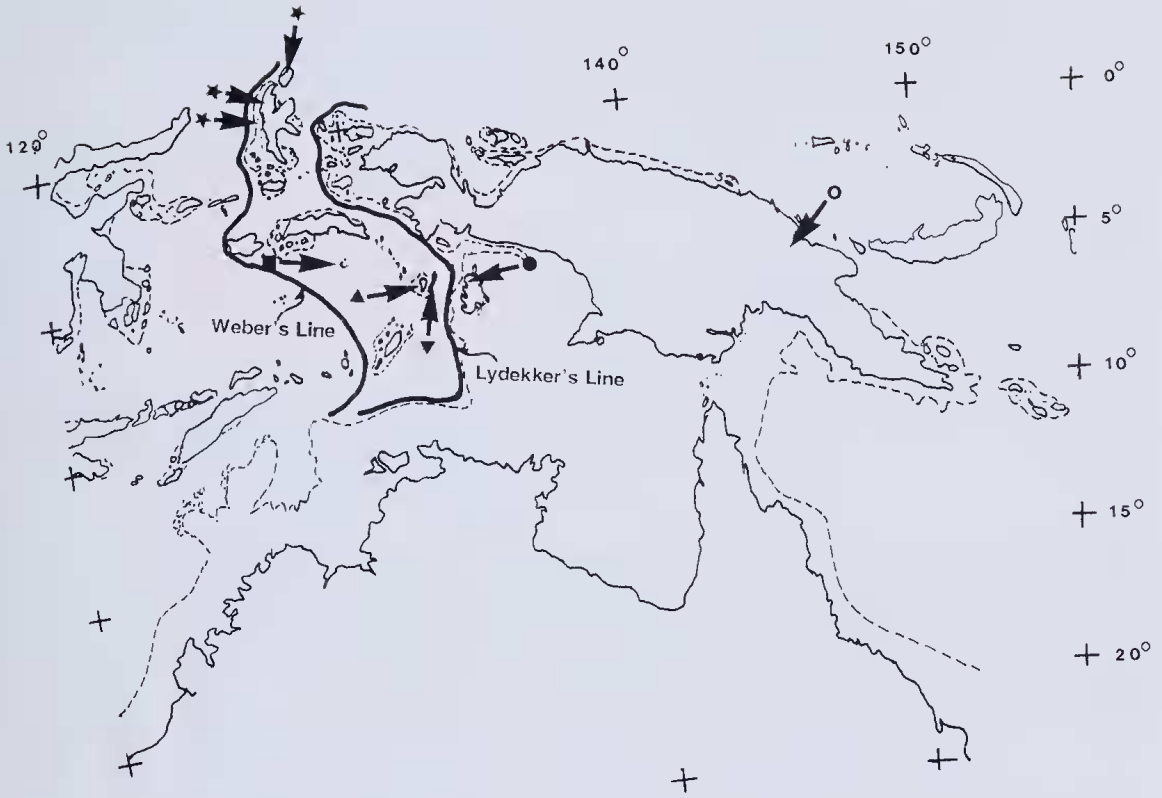

Figure 1 Locality of *Nyctimene albiventer* in this study. *N. albiventer keasti* subsp. nov. from Kai Kecil (▲), Kai Besar (▼) and Banda Neira (■); *N. albiventer albiventer* from Halmahera group (★); *N. albiventer papuanua* from Aru islands (●); and *N. albiventer papuanus* from Papua New Guinea (O). Also shown are the boundaries of the Sahul Shelf (dotted) and both Weber's and Lydekker's Biogeographic line (broad lines).

Seventeen measurements of skull, dentary and dental characters and 8 of external characters (all in mm) were recorded from adult specimens.

The measurements recorded were (all measurements involving teeth are to alveoli): GSL, greatest skull length; CBL, condylobasal length, PIF, minimum length from posterior margin of incisive foramen to margin of posterior palate; RL, rostrum length, from anteromost internal margin of orbit to nares; RH, rostrum height, from upper canine alveoli to level of dorsal surface of nasals; BB, braincase breadth above zygoma; ZW, zygomatic width; M^1M^1 and C^1C^1, width across M^1M^1 and C^1C^1 respectively, from the labial side; C^1M^1 and C_1M_2 upper and lower canine to last molar length; IOB, minimum interorbital breadth; POB, minimum postorbital breadth; MFW, mesopterygoid fossa width, at the widest point of the palatal flange; P^4P^4, palatal width between the lingual aspect of P^4P^4; ML, mandible length, from condyle to anteromost point of dentary; CH, dentary coronoid height; SV, tip of rhinarium between nostrils to anus length; TV; tail to anus length; EAR, basal notch to apex length; PES, length of pes, angle joint to tip of finger, excluding claw; FA, forearm length; MC3-5, metacarpal 3,4 and 5 length.

Table 1 Measurements, in mm, for skull, dentary, dental and external characters (see Material and Methods for explanation of character codes) of adult *Nyctimene albiventer albiventer* (Morotai I; Ternate islands and Halmahera I.), *N.a. papuanus* (Wokam islands, Aru; Papua New Guinea) and *N. a. keasti* subsp. nov. (Dullah I., Kai Kecil I. Kai Besar I. and Neira Banda I., Banda islands). N, sample size; $\bar{X}$, mean; SD, standard deviation; Min, minimum; Max., maximum.

		GSL	CBL	PIF	RL	RH	BB	ZW	M^1M^1	C^1C^1	C^1M^1	IOB
Nyctimene a. keasti	N	7	7	7	7	7	7	7	7	7	7	7
Kai Kecil I.	$\bar{X}$	28.81	27.37	12.09	5.46	6.49	12.17	19.02	8.13	5.48	9.50	5.69
(Pulau Dullah)	SD	0.50	0.42	0.28	0.34	0.36	0.31	0.36	0.28	0.26	0.26	0.28
	Min	28.04	26.56	11.58	4.96	5.98	11.64	18.63	7.66	5.21	8.98	5.29
	Max	29.38	27.88	12.47	5.90	6.96	12.56	19.71	8.45	5.78	9.80	6.12
Nyctimene a. keasti	N	5	5	5	5	5	5	5	5	5	5	5
Kai Besar I.	$\bar{X}$	28.71	27.15	12.01	5.60	6.17	12.56	19.11	8.19	5.44	9.67	5.68
	SD	0.54	0.67	0.26	0.35	0.34	0.09	0.31	0.18	0.23	0.17	0.20
	Min	28.22	26.02	11.72	5.05	5.75	12.44	18.88	7.91	5.18	9.36	5.50
	Max	29.36	27.69	12.42	6.00	6.66	12.68	19.60	8.40	5.80	9.77	5.98
Nyctimene a. keasti	N	2	2	2	2	2	2	2	2	2	2	2
Banda I.	$\bar{X}$	29.05	27.84	11.99	5.67	6.40	12.61	19.38	8.50	5.24	9.46	5.31
	SD	0.27	0.28	0.03	0.18	0.02	0.43	0.12	0.11	0.38	0.13	0.03
	Min	28.86	27.64	11.97	5.54	6.39	12.30	19.30	8.42	4.97	9.37	5.29
	Max	29.24	28.04	12.01	5.80	6.42	12.91	7	8.58	5.51	9.55	5.33
Nyctimene a. keasti	N	14	14	14	14	14	14	14	14	14	14	14
(Total)	$\bar{X}$	28.81	27.36	12.05	5.54	6.37	12.37	19.10	8.21	5.43	9.56	5.63
	SD	0.47	0.53	0.24	0.32	0.35	0.32	0.33	0.25	0.26	0.22	0.26
	Min	28.04	26.02	11.58	4.96	5.75	11.64	18.63	7.66	4.97	8.98	5.29
	Max	29.38	28.04	12.47	6.00	6.96	12.91	19.71	8.58	5.80	9.80	6.12
Nyctimene a. albiventer	N	6	6	5	6	6	6	6	6	6	6	6
Moratai I. Ternate I.	$\bar{X}$	25.68	24.55	10.27	4.83	5.80	11.36	17.01	7.32	4.82	8.49	4.90
Halmahera I.	SD	0.60	0.60	0.43	0.10	0.20	0.15	0.29	0.19	0.12	0.17	0.28
	Min	24.67	23.75	9.83	4.69	5.57	11.10	16.55	7.02	4.68	8.24	4.47
	Max	26.39	25.17	10.93	4.97	6.02	11.54	17.36	7.50	5.01	8.69	5.27
Nytcimene a. papuanus	N	13	13	13	13	13	13	13	13	13	13	13
Papua New Guinea	$\bar{X}$	26.82	25.69	10.57	4.60	6.41	12.00	18.27	7.98	5.17	8.63	5.21
	SD	0.50	0.53	0.45	0.27	0.23	0.35	0.44	0.25	0.11	0.21	0.24
	Min	25.86	24.73	9.77	4.08	5.94	11.40	17.40	7.46	5.03	8.20	4.83
	Max	27.41	26.37	11.25	5.02	6.73	12.60	19.18	8.28	5.41	9.02	5.51
Nyctimeme a. papuanus	N	26	26	26	26	26	26	26	25	26	26	26
Aru islands	$\bar{X}$	27.35	26.06	10.72	4.79	6.26	12.03	18.22	8.23	5.35	8.99	4.99
	SD	0.68	0.70	0.48	0.27	0.36	0.34	0.53	0.34	0.26	0.28	0.33
	Min	25.84	24.45	9.74	4.37	5.48	11.55	17.46	7.69	4.97	8.43	4.48
	Max	28.45	27.40	11.68	5.38	7.00	13.06	19.69	9.22	6.10	9.51	5.73

The skull, dentary and dental characters were measured to 0.01, while the external characters were measured to 0.1. Terminology used in the description of skull, dentary, dental and external characters follows Hill and Smith (1984). Pelage description follow the colour terminology of Smithe (1975).

Table 1 (cont.)

POB	MFW	P^4P^4	ML	CH	C_1M_2	SV	TV	EAR	PES	FA	MC3	MC4	MC5
7	7	7	7	7	7	7	7	7	7	7	7	7	7
5.88	4.70	5.18	21.38	12.80	10.81	74.5	21.4	15.3	12.5	58.4	42.0	38.6	4.08
0.37	0.15	0.09	0.42	0.28	0.32	3.1	1.6	0.3	0.8	0.8	1.0	0.9	0.9
5.21	4.50	5.03	20.69	12.42	10.27	69.9	19.9	14.8	11.6	57.1	40.7	37.5	39.4
6.27	4.96	5.29	22.03	13.22	11.18	78.7	24.1	15.6	13.9	59.4	43.2	39.6	41.8
5	5	5	5	5	5	5	5	5	5	5	5	5	5
6.20	4.84	5.22	21.64	12.94	10.89	73.8	19.7	14.4	13.4	57.9	42.4	38.4	40.5
0.24	0.17	0.13	0.63	0.37	0.16	5.6	0.8	0.3	0.3	1.8	1.4	0.6	1.5
5.83	4.69	5.06	20.58	12.33	10.75	69.7	18.6	14.2	13.1	55.1	40.9	37.7	38.7
6.44	5.05	5.38	22.11	13.32	11.10	83.3	20.9	14.8	13.8	59.7	44.3	39.4	42.7
2	2	2	2	2	2	2	2	2	2	2	2	2	2
5.89	4.78	5.37	21.13	12.42	10.88	69.8	22.6	14.9	12.5	60.6	42.2	38.6	39.9
0.17	0.14	0.25	0.19	0.25	0.2	0.6	3.1	0.1	1.7	2.6	2.4	2.6	1.8
5.77	4.68	5.19	20.99	12.24	10.76	69.3	20.4	14.8	11.3	58.7	40.5	36.7	38.6
6.01	4.88	5.55	21.26	15.59	11.00	70.2	24.8	14.9	13.7	62.4	43.9	40.4	41.2
14	14	14	14	14	14	14	14	14	14	14	14	14	14
6.00	4.76	5.22	21.44	12.80	10.85	73.5	20.9	14.9	12.8	58.5	42.2	38.5	40.5
0.33	0.16	0.14	0.49	0.34	0.24	4.1	1.8	0.5	0.9	1.6	1.2	1.0	1.2
5.21	4.50	5.03	20.58	12.24	10.27	69.3	18.6	14.2	11.3	55.1	40.5	36.7	38.6
6.44	5.05	5.55	22.11	13.32	11.18	83.3	24.8	15.6	13.9	62.4	44.5	40.4	42.7
6	5	6	6	6	6	6	6	6	6	6	6	6	6
5.33	4.64	4.65	18.97	10.31	9.52	69.8	20.9	12.7	11.0	51.2	36.1	33.8	35.1
0.27	0.22	0.14	0.55	0.54	0.13	2.0	2.2	0.4	0.7	1.2	0.8	0.8	0.9
4.96	4.27	4.50	18.07	9.56	9.31	67.5	19.3	12.1	10.3	49.9	35.0	32.4	34.3
5.64	4.82	4.83	19.50	10.78	9.69	73.6	25.2	13.3	12.1	53.1	37.2	34.5	36.5
13	13	12	13	13	13	15	15	15	15	15	15	15	15
5.76	4.66	5.24	19.76	11.22	9.61	70.6	20.7	12.8	10.7	54.6	39.2	36.2	38.7
0.34	0.19	0.26	0.41	0.29	0.37	3.3	1.5	0.8	0.6	1.2	1.2	0.7	1.1
5.14	4.37	4.71	19.14	10.74	9.01	64.2	19.1	11.7	9.9	52.7	37.4	35.0	36.5
6.38	4.95	5.58	20.53	11.70	10.17	74.7	23.4	14.2	12.2	56.8	40.9	37.7	4.03
26	26	25	25	26	25	27	27	27	27	27	27	27	27
5.54	4.48	5.36	20.26	11.69	9.99	65.8	22.3	13.6	12.2	55.8	39.8	36.1	39.0
0.36	0.27	0.24	0.67	0.73	0.36	5.4	2.5	0.8	0.7	1.6	1.6	1.4	1.4
4.92	4.06	4.97	18.09	10.32	9.43	57.9	17.9	11.7	11.2	53.4	35.5	33.5	36.0
62.5	5.35	5.87	21.30	12.69	10.67	77.6	30.1	14.7	13.3	59.2	42.8	39.2	41.3

Adults were diagnosed as those specimens with the following sutures fused: basioccipital - basisphenoid, basisphenoid - presphenoid and palatine - maxillary (these sutures are illustrated in Heaney and Peterson 1984: Figure 4).

The effect of sex and island for all characters was examined by multiple regressions for the six

Table 2 Multiple regressions on sex and island populations of *Nyctimene albiventer* (Halmahera group, Kai Kecil, Kai Besar, Banda, Aru and Papua New Guinea) for skull, dentary, dental and external characters. F values are presented for the main effects and their interaction. For explanation of character codes see Material and Methods section. Significance levels are *, $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, *** $p < 0.001$

CHARACTER	MAIN EFFECTS SEX	ISLAND	INTERACTION SEX. ISLAND
GSL	0.389	13.842***	1.076
CBL	1.394	8.652***	1.086
PIF	0.769	12.721***	1.153
RL	0.074	8.775***	1.050
RH	0.001	2.784*	0.436
BB	1.092	3.914**	0.673
ZW	2.627	10.046***	0.360
M^1M^1	0.005	5.203***	0.550
C^1C^1	0.587	4.251**	2.027
C^1M^1	1.382	15.180***	0.200
IOB	0.010	5.912***	0.986
POB	0.001	1.671	1.937
MFW	0.007	1.752	0.181
P^4P^4	0.101	6.404***	0.236
ML	0.146	10.302***	0.799
CH	1.344	10.850***	0.567
C_1M_2	2.071	13.018***	0.737
SV	0.008	5.682***	1.486
TV	1.080	1.228	1.384
EAR	0.659	11.114***	0.336
PES	0.101	13.893***	0.237
FA	0.113	13.042***	0.208
MC3	0.941	11.676***	0.311
MC4	0.456	8.204***	0.307
MC5	2.475	10.962***	0.529

islands/island groups: Banda, Kai Kecil, Kai Besar, Aru, Halmahera group and Papua New Guinea. Examination of the residuals from regression analyses gave no indication of heteroscedasticity.

Stepwise canonical variate (discriminant) analyses were run for skull, dentary and dental characters and external characters using all characters and a reduced set of these characters. This reduced set of characters was selected because they provided values that minimise Wilks Lambda.

STATISTICS: RESULTS AND DISCUSSION

Univariate statistics

Mean, standard deviation, minimum and maximum values and sample size for each island or island group are presented in Table 1 for all characters examined.

Multiple regressions

Multiple regressions were run for skull, dentary and dental and external characters on sex and

island populations for the groups: Kai Besar, Kai Kecil, Banda, Aru, Halmahera and Papua New Guinea (Table 2).

Sex

No character showed a significant relationship with sex alone or with the interaction between sex and island (Table 2).

Island

Only postorbital breadth (POB), mesopterygoid fossa width (MFW) and tail to vent (TV) were not significantly related to island. Rostrum height (RH) was also probably not significantly related to island because $P>0.01$ might be expected to occur by chance alone, considering the number of interactions being tested. The 21 other characters, most of which were significant at $P<0.001$, indicated that there were considerable differences in morphology between these island populations.

Multivariate analyses

Because the multiple regression analysis indicated no sexual dimorphism, males and females are combined in the subsequent analyses.

The DFA was first run using the islands Aru, Kai Besar, Kai Kecil, the Halmahera group (Halmahera, Ternate and Morotai), Papua New Guinea and Banda. Banda was ungrouped because there was only two individuals. Kai Besar, Kai Kecil and Banda clustered closely together, as did Aru and Papua New Guinea. The DFA was then run using the following island groupings representative of putative taxa: Kai Besar/Kai Kecil/Banda, Aru/Papua New Guinea and the Halmahera group, for skull, dentary and dental characters and externals characters separately. These analyses used the complete set of 17 skull, dentary and dental characters and 8 external characters.

However, because the number of individuals in the island group with the smallest sample size (the Halmahera group, N=6) was less than the number of characters measured, fewer characters were used in the analysis. Only the DFA based on these reduced character sets are presented below. This was because both for the skull, dentary and dental and external characters, the reduced set of characters produced very similar DFA plots to those using the full set of characters.

Skull, dentary and dental characters

The DFA was run using the following characters: greatest skull length (GSL), inside P^4P^4 breadth (P^4P^4) lower C_1M_2 length (C_1M_2) and rostrum length (RL). The DFA produced two significant functions. Function 1 explained 63.4 percent of the variance and function 2, 36.6 percent. A total of 98.3 percent of individuals were correctly classified to their appropriate island group. The misclassified animal was from Aru; it was placed in the Halmahera group. the plot of functions 1 and 2 (Figure 2a) indicates that the island groups were approximately equidistant in discriminant function space. The Kai islands/Banda group separated from both the other two island groups on function 1 and from the Halmahera group on function 2. The Halmahera group also separated from the Aru/Papua New Guinea group on function 2.

The characters loading most heavily (>0.6) on function 1 were C_1M_2 and RL (Table 3a). Characters loading heavily (>0.6) on function 2 were GSL and P_4P_4 (Table 3a).

External characters

The DFA was run using the following characters: forearm length (FA) ear length (EAR), snout to vent length (SV) and pes length (PES). The DFA produced two significant functions. Function

Table 3 Canonical variate function coefficients for the *Nyctimene albiventer* subspecies (*albiventer*, *papuanus* and subsp. nov.). Standardised values, followed by (in brackets) unstandardised values. (a) skull and dental characters and (b) external characters. For explanation of character codes see Materials and Methods section.

Table 3a

CHARACTER	FUNCTION 1	FUNCTION 2
GSL	-0.1618 (-0.2569)	1.0604 (1.6839)
P^4P^4	-0.4071 (-1.8559)	0.6624 (3.0199)
C_1M_2	0.8256 (2.3241)	-0.2980 (-0.8388)
RL	0.7687 (2.7696)	-0.5667 (-2.0418)
CONSTANT	-20.3478	-43.4262
VARIANCE EXPLAINED (%)	63.4	36.6

Table 3b

CHARACTER	FUNCTION 1	FUNCTION 2
FA	0.6331 (0.4091)	-0.8306 (-0.5367)
EAR	0.1260 (0.1385)	0.3754 (0.4125)
PES	0.3406 (0.0708)	0.7559 (0.1571)
SV	0.5169 (0.6720)	0.4953 (0.6439)
CONSTANT	-38.4503	5.3860
VARIANCE EXPLAINED (%)	84.9	15.1

1 explained 84.9 percent of the variance and function 2, 15.1 percent (Table 3b). A total of 91.9 percent of individuals were correctly classified to their appropriate island group. The misclassified animals were as follows: two Aru/Papua New Guinea animals were classified to the Halmahera group and two to the Kai islands/Banda group. The plot of functions 1 and 2 shows that all three groups cluster separately, with the Kai islands/Banda group forming the most distinct cluster. The Kai islands/Banda group separated from both the other island groups principally on function 1. The Aru/Papua New Guinea group separates from the Halmahera group principally on function 2 (Figure 2b). The character that loads most heavily (>0.6) on function 1 is FA and those that load most heavily (>0.6) on function 2 are FA and PES.

The above DFA indicates that Kai Besar, Kai Kecil and Banda islands have a population of *Nyctimene* that differs in morphology from that on the Aru islands. The *Nyctimene* from the Kai islands were considered by Andersen (1912) and Laurie and Hill (1954) to be *N. albiventer papuanus* (Andersen 1912 examined at least one specimen from Elat, Kai Besar in his critical revision). Our comparison with *N. a papuanus* from Papua New Guinea indicates that it is the Aru population that is most similar to *N. a. papuanus*, and not the Kai islands/Banda populations. Further, comparison with topotypical specimens of *N. a. albiventer* from Morotai and the other islands on which this form is distributed (Halmahera and Ternate) indicates that the Kai islands/Banda population is not representative of *N. a. albiventer*. Comparison of the Kai islands/Banda I. population with the other small forms of *Nyctimene*, indicates that is an undescribed subspecies of *Nyctimene albiventer* which is described below.

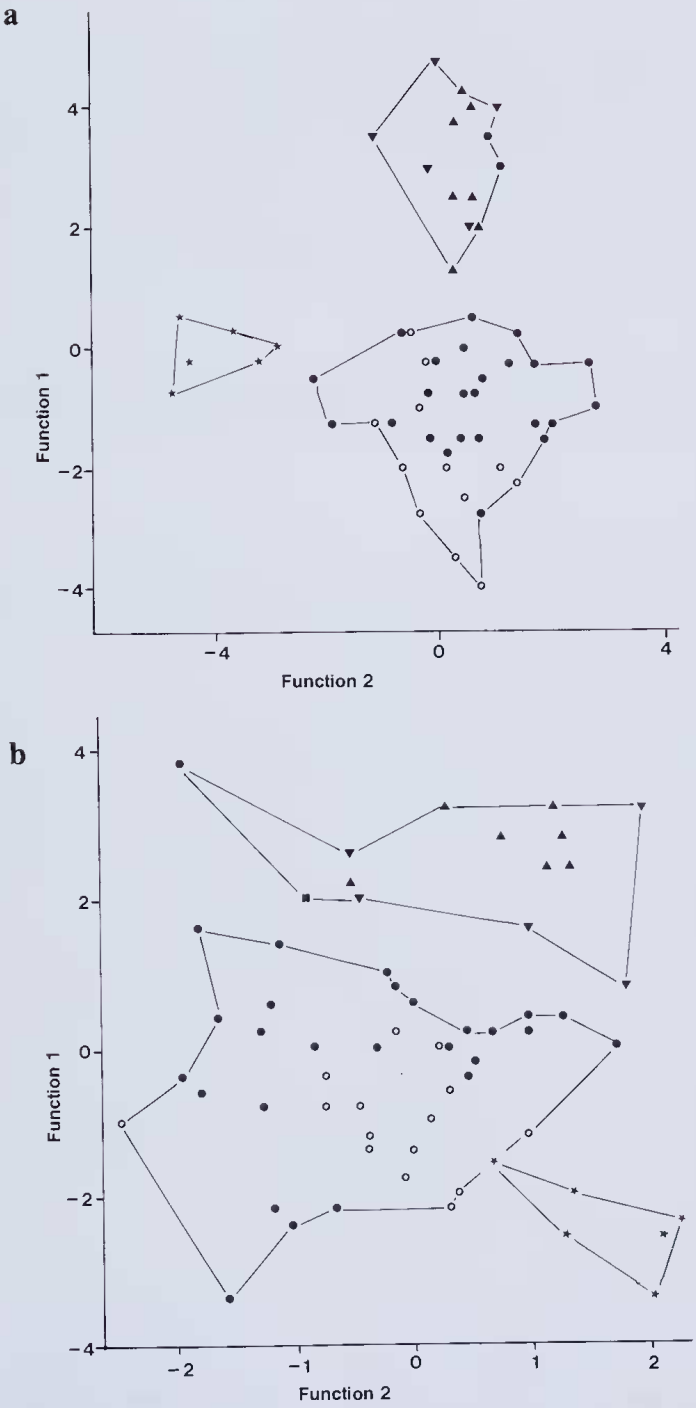

Figure 2 Canonical variate analysis based on three island groupings of (Kai islands/Banda group, Halmahera/Morotai/Ternate group and Aru/Papua New Guinea group) based on (a) skull, dentary and dental characters and (b) external characters, for functions 1 and 2. Symbols for *N. albiventer* subspecies as for Figure 1 caption.

SYSTEMATICS

Nyctimene albiventer keasti Kitchener, subsp. nov.

Holotype

Museum Zoologicum Bogoriense No. MZB 15300; adult male; weight 30 gm; carcase fixed in 10 percent formalin, preserved in 75 percent ethanol; skull separate; collected by D.J. Kitchener and R.A. How on 22 October 1992.

Type locality

Near Taman Anggrek, 12 km N. Tual, Pulau Dullah, closely associated with Pulau Kai Kecil, (5°38'S,132°44'E), collected in a mist net from mixed lowland evergreen rainforest bordering a lake, at sea level.

Paratypes

Kai islands, Dullah I., (nr. Kai Kecil), Nr Taman Anggrek (05°03'S, 132°44'E.): WAM M42141-2, M42144-5, M42649, M42651 (5♂♂, 1♀); Kai islands, Kai Besar, Desa Mun (05°26'S, 133°04'E.): WAM M42054, M42090 (1♂, 1♀); Elat (05°39'S, 132°59'E.): WAM M42686 (1♂); 3 km W Fakoi (05°36'S,133°06'E.) WAM M42699-700 (2♂♂); Banda islands, Banda Neira I. (04°33'S, 129°55'E.): WAM M42006, M42375 (2♀♀).

Diagnosis

Nyctimene albiventer keasti is compared directly with *N.a albiventer, N. a. papuanus* and *Nyctimene cephalotes* (WAM specimens from Ambon and Seram). It is compared with *N. minutus, N. cyclotis, N. masalai* and *N. vizcaccia* through the excellent description of these forms in Andersen (1912), Smith and Hood (1983), and Heaney and Petersen (1984), and also utilising Corbet and Hill (1992).

Nyctimene albiventer keasti differs from *N. a. albiventer* in having females that have a considerably paler dorsal pelage (Fawn Color) than males (Buff Yellow). In averaging larger in all measurements, except tail to vent length (Table 1). It is absolutely larger in the following characters: greatest skull length 28.81 (28.04-29.38) *v.* 25.68 (24.67-26.39), zygomatic width 19.10 (18.63-19.71) *v.* 17.01 (16.55-17.36); mandible height 12.80 (12.24-13.32) *v.* 10.31 (9.56-10.78), C_1M_2 length 10.85 (10.27-11.18) *v.* 9.52 (9.31-9.69), forearm length 58.5 (55.1-62.4) *v.* 51.2 (49.9-53.1) and ear length 14.9 (14.2-15.6) *v.* 12.7 (12.1-13.3).

It differs from *N. a papuanus* from Papua New Guinea by averaging larger in most measurements and having the following measurements absolutely larger: greatest skull length, palate to incisor foramen length, mandible length, mandible height, C_1M_2 length and metacarpal 4 length (Table 1).

It differs from *N. a. papuanus* from Aru islands in averaging larger in all measurements except P^4P^4 length and tail to vent length. For example: greatest skull length 28.81 (28.04-29.38) *v.* 27.35 (25.84-28.45), zygomatic width 19.10 (18.63-19.71) *v.* 18.22 (17.46-19.61), mandible height 12.80 (12.24-13.32) *v.* 11.69 (10.32-12.69), C_1M_2 10.85 (10.27-11.18) *v.* 9.99 (9.43-10.67), forearm length 58.5 (55.1-62.4) *v.* 55.8 (53.4-59.2) and ear length 14.9 (14.2-15.6) *v.* 13.6 (11.7-14.7)

It further differs from *N. a. papuanus* from Aru (generally) and Papua New Guinea (absolutely) in having the greatest skull length larger relative to P^4P^4 breadth (Figure 3a); rostrum length generally longer relative to P^4P^4 breadth (Figure 3b) and ear length generally longer relative to forearm length in both the Aru and Papua New Guinea populations (Figure 4).

It differs from both *N. a albiventer* and *N. a. papuanus* by clustering distinctly from them in discriminant function space for both skull, dentary and dental characters and external characters. (Figures 2a, b).

It differs from *N. cephalotes* in having dorsal stripe less obvious, particularly on anterior one-

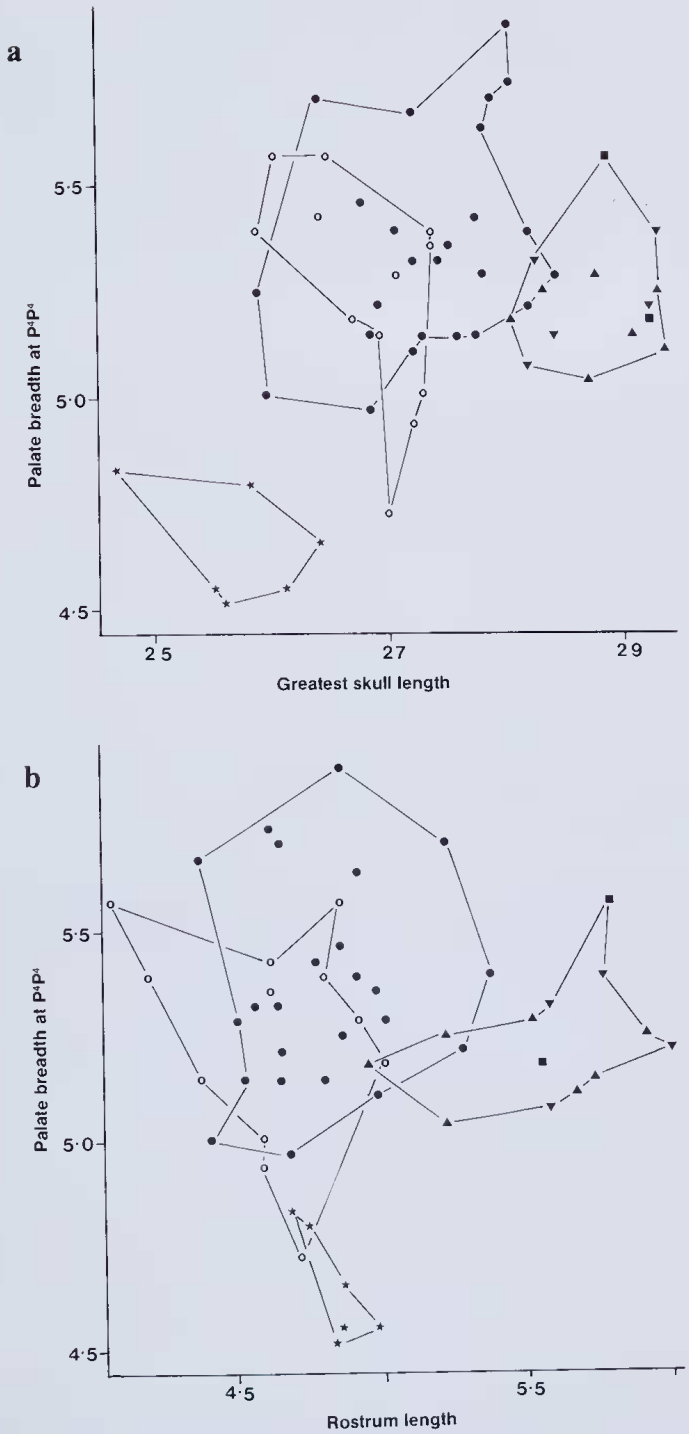

Figure 3 Plot of palatal width at P^4P^4 versus (a) greatest skull length and (b) rostrum length for subspecies of *Nyctimene albiventer*. Symbols as for Figure 1 caption.

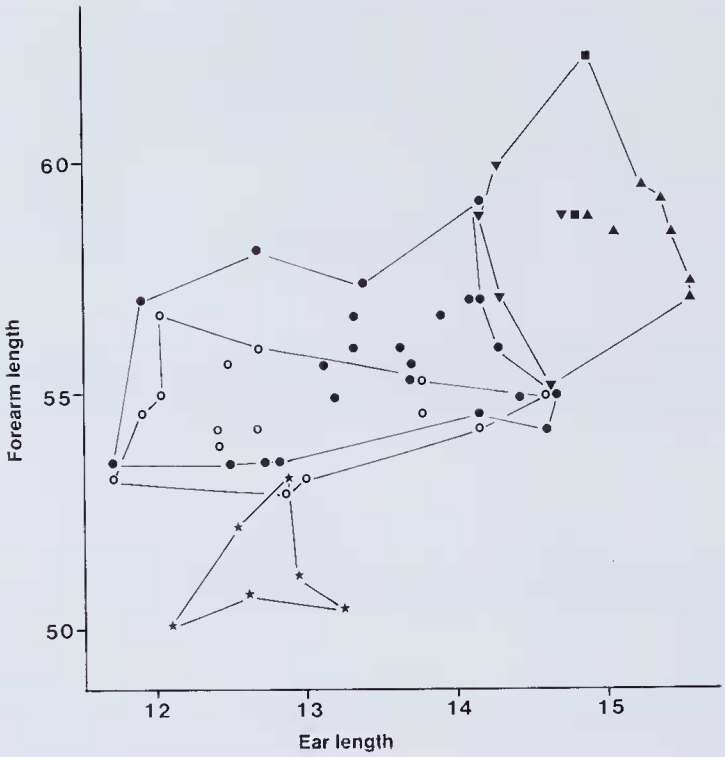

Figure 4 Plot of forearm length *versus* ear length for subspecies of *Nyctimene albiventer*. Symbols as for Figure 1 caption.

third of back, and narrower 1.0-3.5 *v.* 3.5-5.0; generally smaller in overall size, for example: condylobasal length 27.36 (26.02-28.04) *v.* 28.1-32; braincase breadth 12.37 (11.64-12.91) *v.* 13.2-13.8; M^1M^1 breadth 8.21 (7.66-8.58) *v.* 9-10; C^1C^1 breadth 5.43 (4.92-5.80) *v.* 5.8-6.2; mandible length 21.44 (20.58-22.11) *v.* 23.0-24.8; forearm length 58.5 (55.1-62.4) *v.* 60-71 (only one specimen from Banda I., had a forearm in excess of 60).

It differs from *N. minutus* in having dorsum generally a uniform colour, except for the presence of a thin dorsal stripe, rather than a conspicuously mottled dorsum with darker tips to the hairs; forearm longer 58.5 (55.1-62.4) *v.* 51-55; metacarpal 3 longer 42.2 (40.5-44.5) *v.* 35.5-38.5; M^1M^1 width larger 8.21 (7.66-8.58) *v.* 7.5; interorbital breadth larger 5.63 (5.29-6.12) *v.* 4.8-5.2; palatal breadth between P^4P^4 5.22 (5.03-5.55) *v.* 4.2-4.4.

It differs from *N. cyclotis* in having ears unmodified rather than unusually broad, semicircularly rounded above; colour of dorsum uniform, except for the presence of a thin dorsal stripe rather than mottled with darker tips to the hairs, pelage not long and woolly; M^1 subequal in size rather than noticeably smaller than P^4; premolars and molars rectangular rather than round; premolars have two strong cusps not three; palate frequently with round fenestrations; forearm longer, averages 58.5 *v. ca.* 53; metacarpal 5 longer 40.5 (38.6-42.7) *v.* 36.5; and interorbital breadth larger 5.63 (5.29-6.12) *v.* 4.5.

It differs from *N. masalai* in having general colour of dorsum uniform rather than mottled dark reddish brown; dark mid dorsal stripe narrower, *ca.* 1.5-3.5 *v.* 5; frontal sinuses converging in supraorbital region rather than parallel; maxillary toothrow slightly to moderately arched rather

than straight; bony palate only slightly domed; no marked reduction of coronial cusps; labial cusps present on C^1 rather than absent; generally smaller in overall size, for example: condylobasal length 27.36 (26.02-28.04) *v.* 29.7-30.7; zygomatic width 19.1 (18.63-19.7) *v.* 20.4-20.9; C^1M^1 length 9.56 (8.98-9.80) *v.* 10.4-10.9; C_1M_2 length 10.85 (10.27-11.18) *v.* 12.1-12.5; and length of forearm 58.5 (55.1-62.4) *v.* 63.5-67.5.

If differs from *N. vizcaccia* in having colour of dorsum generally uniform rather than mottled, cranium squarish rather than rectangular; braincase globose rather than elongate, rostrum shorter (Smith and Hood 1983: figures 1,2); P3 with distinct internal cusp teeth, usually shorter.

Description

Skull, dentary and dentition

Rostrum of skull short, nasal dorsal surface almost horizontal, premaxillary part of nares terminates directly above incisors or projects slightly anterior to them; braincase typical of *N. albiventer* with cranium inflated to level of frontal dorsal inflation, or just above that level, generally less inflated than in *N. albiventer*; zygoma wide; intraorbital foramen suboval and traverse lower half of zygomatic arch; frontals low to arched, depending on age, occasionally with pronounced frontal sulcus, converging slightly posteriorly; sagittal and lambdoidal crests moderately high, the junction of these crests projects posteriorly to a point approximately level with supraoccipital; posterior palate extends well beyond M^1, its margin varies from U-shaped to sharply rectangular; basi-and presphenoid median ridge prominent; pterygoid process low and slightly arched ventrally towards the mesoptergoid fossa.

Upper toothrows gently curved; upper incisors in contact, sited posterior of line joining C^1C^1 anteriormost face, except for Banda specimens which approach this line; C^1 with moderate secondary labial cusp, this cusp not apparent in some old specimens with worn teeth, prominent cusp with gentle lingual ridge connecting to lingual and posterior cingulum. P^2 subcircular, buccal area half to three-quarters that of incisors; P^3 occlusal view shape rectangular with a prominent labial cusp and much lower separate lingual cusp; posterior basal shelf well defined and forms slight basin, occlusal area slightly larger than P^4; P^4 occlusal view subrectangular with posterolingual salient from basal shelf, labial cusp lower than that of P^3, lingual cusp less clearly defined than that of P^3 with longer posterior ridge that reaches almost to posterolingual edge of posterior basal shelf, lingual cusp closer in height to labial cusp than is case in P^3, M^1 subrectangular, labial cusp low and only slightly taller than lingual cusp, posterior basal shelf definition similar to that of P^3 and P^4. C_1 not in contact with each other or with P_2; P_2 suboval, slightly taller than C_1 cingulum; P_3 with tall labial cusp with gently sloping anterior and posterior flanges in line of toothrow, shorter labial cusp distinct; P_4 considerably shorter than P_3, labial cusp taller than lingual cusp but less so than in P_3. These cusps connected by commissure that arcs around the anterior face of tooth; M_2 longer and narrower than P_4 but with both labial and lingual cusps much reduced on those of P_4; M_2 small, about half area of M_1 when viewed from occlusal aspect, posterior basal shelf slightly smaller than that of P_4 and M_1.

Pelage

In males, dorsal pelage considerably darker than that of females. In males, dorsal fur predominantly Fawn Color, ca 10.5 long, with basal one-third of hairs Drab. A moderately wide dorsal stripe of Olive Brown begins thinly (0.5-1.5 wide) at the neck and widens to 3.5 in region of lower back; fur on dorsal proximal surface of uropatagium Fawn Color. Throat, chest and

abdomen Buff Yellow, ca 5.5 long; underside of shoulder Cinnamon; ears not furred, distal three-quarters Burnt Umber and remainder Cinnamon.

In females, dorsal fur predominantly Buff Yellow with basal one-third of hairs Drab; dorsal median stripe as for males and Olive Brown; fur on dorsal proximal surface of uropatagium Raw Umber. Throat, chest and abdomen Buff Yellow; Ears not furred, distal half Burnt Umber and remainder Clay Color.

Both sexes have wings and ears with yellow spots of varying size, these spots are generally confined to skin of forearm and digits and occasionally tibia and tail. The wing patagia have darker spots of irregular size.

Distribution

Banda and Kai Island groups.

Etymology

Named after Mr Colin Keast, Western Australian Museum, who has assisted in an honorary capacity over a period of three years with laboratory aspects of the research in the Indonesian mammals. These animals were collected as a consequence of the joint Western Australian Museum and Museum Zoologicum Bogoriense expeditions to Eastern Indonesia.

GENERAL DISCUSSION

Simpson (1977) reviewed the biogeography of Wallacea (incorporating the Maluku islands) and concluded that it was not a region of intergradation between the faunas on the Sahul Shelf to the east and the Sunda Shelf to the west. Rather, he considered it to be a region with a considerable extent of endemicity and possessing its own unique fauna. Recent studies on mammals in Nusa Tenggara on the southern edge of Wallacea support this view (Kitchener *et al.* 1993).

It appears from the detailed critique offered by Simpson (1977) on the biogeography of this broad region, that the eastern boundary for mammals between Wallacea and the Australian Biogeographic region is placed somewhere between Lydekker's (1896) Line and Weber's Line as defined by Mayr (1944) (see Figure 1). Lydekker's Line follows the western boundary of the Sahul Shelf whereas Weber's Line lies considerably to the west, between Babar and Tanimbar islands north to the western side of Buru I. and the Halmahera group of islands.

As noted by Simpson (1977) Lydekker's Line, readjusted to coincide with the edge of the Sahul Shelf, is a "clear cut boundary". All faunas and islands to east of that line definitely belong to the Australian Region. However, Mayr (1944) proposed, based on "faunal balance", that Weber's Line represented the boundary where the Oriental and Australian fauna meet. Although this view was criticised by Simpson (1977), it does indicate that a considerable number of Australian animal species reach Weber's Line. Clearly, then, the zone between Lydekker's and Weber's Lines represent a zone of interface between the Australian Region and the regions to the west. Further, this interface zone would appear to offer considerable opportunities for research as to the possible mechanisms (morphological, genetic and ecological) at play that restrict the distribution westwards of the Australian fauna.

This study of the morphological variation within *Nyctimene albiventer* indicates that while the population on Aru is similar to that of Papua New Guinea (*N. a. papuanus*), the populations on Kai Besar, Kai Kecil and Banda islands are morphologically distinct (*N. a. keasti* subsp. nov.) as are those of the Halmahera group (*N. a. albiventer*). Other species of mammals which have forms

on both Aru and Kai islands that have been recognised as taxonomically distinct are: *Syconycteris australis* Peters, 1867; *Rhinolophus euryotis* Temminck, 1834; *Hipposideros ater* Templeton, 1848; *Pteropus melanopogon* Peters, 1867; *Phalanger orientalis* (Pallas, 1766) and *Thylogale brunii* (Schreber, 1778) (see Appendix). Both the Kai islands forms of *Syconycteris australis* and *Thylogale brunii* were considered by van Strien (1986) to be the same subspecies as those on Aru islands. However, the form of *Syconycteris australis, Phalanger orientalis* and *Thylogale brunii* on Aru islands was considered the same as those in New Guinea, while the Kai islands form was distinct. (The Kai islands form of *P. orientalis* also occurs on Banda islands.).

During the last major glaciation (17000-20000 yr BP), the sea levels in the northern Australasian region were 120-145 m lower than at present (Chappell 1982: 69). This resulted in the exposure of the Sahul Shelf, including the area of the Arafura Sea. Such exposure of the Sahul Shelf has occurred for extensive periods of the geological history of this region since the Triassic (Doutch 1972). Thus the Aru islands were connected by dry land to New Guinea intermittently throughout the Pleistocene. However, during this period, the Aru islands were separated from Kai islands and Banda islands by a water gap similar in width to the present one (see Figure 1). As a consequence of past connections, the mammal fauna of the Aru islands has been greatly influenced by that of New Guinea, as suggested by the distribution pattern of subspecies cited above. Reference to the Appendix, which lists the species on Aru, Kai and Banda islands, with each species categorised as being essentially Australian (A), Oriental (O), endemic (E) or of uncertain origin (U), further attests to this association.

On Aru islands, all 16 marsupial and rodent species, including a suite of New Guinea lowland murids recorded there for the first time by us (*Rattus steini, R. leucopus, Melomys rufescens* and *M.* sp. cf. *M. levipes*), are New Guinea in origin - as are three of the six bat species. The two shrews and the civet cat are Oriental. There are no endemic species. Thus of the 25 mammal species on Aru that can be categorised, 76% are Australian and 24% are Oriental in origin.

On Kai islands, six of the seven marsupial and rodent species and five of the ten bat species are Oriental. The shrew and the civet cat are Oriental. Two and possibly three species are endemic including a newly described *Melomys* (Kitchener and Maryanto 1993). The taxonomic situation with *Rhinolophus keyensis* is still unclear. Thus of the 19 mammal species on the Kai islands that can be categorised 58% are Australian and 42% are Oriental.

On the Banda islands only two of the eight species (25%) that could be categorised are Australian.

Of particular interest biogeographically was the discovery of the shrew species *Suncus murinus* (Linnaeus, 1766) on Banda Neira I.; Kai Besar I. and Wokam I., Aru islands and *Crocidura maxi* (Sody, 1936) on Wokam I., Aru I. These are the most eastern records of shrews reported in the Indo-Malayan region (see Corbet and Hill 1992) and are the first records of shrews on the Sahul Shelf. The specimens of *Crocidura maxi* vary slightly both genetically and morphologically, from *C. maxi* reported elsewhere in the Lesser Sunda islands. (Kitchener *et al.* 1993). This finding is of interest because it is the only known location where shrews coexist with a small Australopapuan carnivorous marsupial (*Sminthopsis virginiae rufigenis*).

In summary, for mammals the Aru and Kai islands lie in the Australian Biogeographic region, while the situation with Banda islands is less clear. Either the deep water gap between oceanic Kai islands and the continental Aru islands, or their different environments or habitats, have been a major impediment to the western movement of the mammal fauna of the Australian region (New Guinea), and possibly to gene flow within species. This is indicated by three situations: first by the proportions of Australian region mammal species on these islands, which falls from 76% of

the fauna on Aru to 58% on Kai islands and 25% on the Banda islands (these values are very slightly increased if *Suncus, Paradoxurus* and *Cervus* are removed from the analysis because they may have been transported around by humans - see Laurie and Hill 1954 and Corbet and Hill 1992); secondly, by the association of subspecies; those on the Aru islands associate with New Guinea, while those on Kai islands associate with the Banda and Maluku populations; and thirdly, Aru islands have no known endemic species, whereas Kai islands have two and possibly three.

SPECIMENS EXAMINED

Nyctimene albiventer papuanus

Aru islands, Wokam I., Kampong Karangguli (05°48'S, 134°15'E.) WAM M42467, M42486, M42498-501, M42556-9, M42605-6, M42562-4, M42577-8, M42585-9, M42590, M42602, M42607-8, M42609 (17♂♂, 10♀♀).

Papua New Guinea

Sempi (5°40'40"S, 145°46'40"E): WAM M427391; Usino (5°33'50"S, 145°21'20"E): WAM M27401-6 (3♂♂, 3♀♀); Baiteta (5°00'20"S, 145°44'40"E): WAM M27398-400 (3♂♂) and Baumina (5°29'00"S, 145°43'00"E): WAM M27392-4, M27397 (3♂♂, 1♀).

Nyctimene albiventer albiventer (All specimens from Australian Museum)

North Halmahera I., Goal area (1°15'N, 127°32'E): M25078, M25080, M25086 (3♂♂); Ternate I., Ayr Tege Tege (0°48'N, 127°20'E): M25085 (1♀); Morotai (20°20'N, 128°20'E): M26457-8 (1♂, 1♀).

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We are grateful to Dr Tim Flannery, Australian Museum for the loan of specimens of *Nyctimene* from Ternate, Morotai and Halmahera islands. Expedition costs were defrayed by grants to D. Kitchener from: National Geographic Society, Washington and Australian National Parks and Wildlife Service, Canberra. Some expenses were borne personally. Garuda Indonesia kindly defrayed freight costs of the expeditions. Mr Colin Keast, Western Australian Museum, removed and cleaned the skulls. Mrs Norah Cooper, Western Australian Museum, ran the computer analyses. Mrs Susan Dalton, Western Australian Museum, typed the manuscript.

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APPENDIX

List of mammal species from Aru, Kai and Banda island groups. N, new records from the Western Australian Museum - Museum Zoologicum Bogoriense survey of October-November, 1992. A, Australian; O, Oriental; U, Biogeographic region not clearly Australian or Oriental; E, endemic.

	SPECIES	ISLAND GROUP ARU	KAI	BANDA
	MARSUPIALIA			
A	*Murexia longicaudata longicaudata* (Schlegel, 1866)	x		
A	*Sminthopsis virginiae rufigenis* Thomas, 1922	x		
A	*Myoictis melas wallacii* Gray, 1858	x		
A	*Echymipera rufescens rufescens* (Peters and Doria, 1875)	x	x	
A	*Phalanger gymnotis* (Peters and Doria, 1875)	x		
A	*P. maculatus chrysorrhous* (Temminch, 1824)	x	x	x
A	*P. orientalis mimicus* Thomas, 1922	x		
U	*P. orientalis amboinensis* (Lacepede, 1801)		x	x
A	*Petaurus breviceps flavidus* Tate and Archbold, 1935	x	xN	
A	*Dactylopsila trivirgata trivirgata* Gray, 1858	x		
A	*Thylogale brunii brunii* (Schreber, 1778)	x		
A	*T. brunii gracilis* Miklouho-Macleay, 1884		x	
	RODENTIA			
A	*Uromys caudimaculatus aruensis*	x	x	
A	*Hydromys chrysogaster beccarii*	x	x	
U	*Rattus rattus sepiticus* Sody, 1933	x	x	x
O	*R. exulans* (Peale, 1848)		xN	xN
A	*R. leucopus* (Gray, 1867)	xN		
A	*R. steini* Ruemmler, 1935	xN		
U	*Mus musculus castaneus*		xN	xN
A	*Melomys rufescens* (Alston, 1877)	xN		
A	*M. sp. cf. M levipes* (Thomas, 1897)	xN		
E	M. sp. nov		xN	
	SORICIDAE			
O	*Suncus murinus* Linnaeus, 1766	xN	xN	xN
O	*Crocidura maxi* Sody, 1936	xN		
	VIVERRIDAE			
O	*Paradoxurus hermaphroditis setosus* Jaquinot and Pucheran, 1853	x	x	
	CERVIDAE			
O	*Cervus timorensis moluccensis* Quoy and Gaimard, 1830			x
	PTEROPODIDAE			
O	*Pteropus melanopogon melanogogon* Peters, 1867			x
O	*P. melanopogon aruensis* Peters, 1867	x		
O	*P. melanopogon keyensis* Peters, 1867		x	
A	*P. macrotis macrotis* Peters, 1867	x	?	
O	*P. griseus* (E. Geoffroy, 1810)			x
O	*Dobsonia viridis viridis* Heude, 1897		x	x
O	*D. moluccense* Quoy and Gaimard, 1830	x		
A	*Nyctimene albiventer keasti* subsp. nov.		x	xN
A	*Nyctimene albiventer papuanus* Andersen, 1910	xN		
U	*Macroglossus minimus lagochilus* Matschie, 1899	x	x	x
A	*Syconycteris australis papuana* (Matschie, 1899)	x		
A	*S. australis keyensis* Andersen, 1911		x	

	SPECIES	ISLAND GROUP ARU	KAI	BANDA
	EMBALLONURIDAE			
O	*Taphozous achates* Thomas, 1915		x	
A	*Emballonura beccarii clavium* Thomas, 1915		x	
A	*E. nigrescens nigriscens* Gray, 1832		x	
	RHINOLOPHIDAE			
U	*Rhinolophus euryotis aruensis* Andersen, 1907	x		
U	*R. euryotis praestans* Andersen, 1905		x	
U	*R. philippinensis achilles* Thomas, 1900	?	x	
E	*R. keyensis keyensis* Peters, 1871		x	
	HIPPOSIDERIDAE			
U	*Hipposideros ater saevus* Andersen, 1918		x	
U	*H. ater aruensis* Gray, 1858	x		
U	*H. cervinus cervinus* (Gould, 1854)	x	x	
O	*H. bicolor* Temminck, 1834		xN	
U	*H. diadema custos* Andersen, 1918		x	
A	*Aselliscus tricuspidatus* Temminck, 1834		x	
	VESPERTILIONIDAE			
U	*Miniopterus australis tibialis* (Tomes, 1858)		x	
O	*M. pusillus macroneme* Revilliod, 1914		x	
U	*M. schreibersii oceanensis* Maeda, 1982		x	
U	*Myotis adversus moluccarum* Thomas, 1915		x	
E	*M. stalkeri* Thomas, 1910		x	
U	*Pipistrellus tenuis papuanus* (Peters and Doria, 1888)	x	x	x
O	*P. javanicus javanicus* (Gray, 1838)	?		
O	*Scotophilus kuhlii temmincki* (Horsfield, 1824)	x		

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